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Proboscis labellar hooks in southern African species of *Sepedon* (Diptera: Schizophora: Sciomyzidae)

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ABSTRACT

It has been speculated that the unusual loss of the ptilinum and ptilinal suture in species of the *Sepedon* lineage is an apomorphy, which correlates with the development of labellar hooks in the proboscis (well-developed hooks are typically absent in other Sciomyzidae). To test this theory, the labellum of four South African species of *Sepedon* was studied using scanning electron microscopy. It was confirmed that all four species have well-developed labellar hooks of various sizes (number of hooks per labellar lobe in parentheses): *S. neavei* Steyskal (7–9), *S. pleuritica* Loew (6), *S. scapularis* Adams (17) and *S. testacea* Loew (17). The labellar hooks are strongly curved and sclerotised, inwardly directed and of similar size and form in all four species. However, in *S. pleuritica*, a remarkable, short, rod-like structure is present at the anteroventral base of each hook. Labellar hooks never arise from the pseudotracheal ring tips, although they are often inserted immediately adjacent to pseudotracheal rows. The apparent form and development of the pseudotracheal rings, and the nature of the interpseudotracheal membrane, are described for all four species. It was estimated that *S. pleuritica*, *S. scapularis* and *S. testacea* each have 15 to 16 pseudotracheae per labellar lobe. Species of *Ditaeniella* Sack and *Ethiolimnia geniculata* Loew, both with the ptilinal suture present, lack labellar hooks, have inconspicuous pseudotracheal rings and a largely undifferentiated interpseudotracheal membrane.

KEY WORDS: Sciomyzidae, *Sepedon*, morphology, ptilinal suture, proboscis, labellar hooks, pseudotracheal rings, interpseudotracheal membrane.

INTRODUCTION

The Sciomyzidae is a cosmopolitan group of schizophoran flies, with a well-documented, yet extraordinary life history. The majority of reared species are consumers of aquatic and terrestrial molluscs, including slugs (Vala *et al*. 2000). Since the malacophagous feeding behaviour of Sciomyzidae was confirmed by Berg (1953), it has been shown that sciomyzid larvae, in the main, kill and feed on aquatic and terrestrial snails, with records also of predation/feeding on slugs, snail eggs and fingernail clams (Barber *et al*. 2004; Knutson & Vala in press).

An incentive for the study of Sciomyzidae in the Afrotropics has been the possibility of using selected species as biocontrol agents of medically and veterinarily important aquatic snails, implicated for example in the transmission of schistosomiasis (see Berg & Knutson 1978; Barraclough 1983). Appleton *et al*. (1994) reviewed and evaluated the use of *Sepedon* Latreille in the control of schistosomiasis in South Africa. Maharaj *et al*. (2005) suggested, based on the feeding behaviour of larvae in the laboratory, that *Sepedon neavei* and *S. scapularis* are potential biocontrol agents of certain aquatic snail species. The genus *Sepedon* dominates the Afrotropical fauna, with more than 40 valid species recorded (Miller 1995).

Since my study on the biology and immature stages of selected species of *Sepedon* in KwaZulu-Natal (Barraclough 1983) was published, very little has been presented on the taxonomy or systematics of adult sciomyzids in southern Africa. This is an obvious impediment to further studies on biology, ecology and behaviour. Barraclough (1985) described two new species of *Sepedon* from South Africa, and Miller (1995) published an identification key to the Afrotropical genera and broadly reviewed the fauna of the Afrotropics.

Recently, however, additional incentives for studies on sciomyzid flies have arisen. It has been suggested that species in the *Sepedon* lineage of genera, all of which have secondarily lost the ptilinum, have developed various morphological and behavioural adaptations to replace the function of this structure (Mc Donnell & Knutson pers. comm.). The ptilinum is an externally eversible sac-like structure. It is well known that it is protruded from the head of schizophoran flies at the time of emergence from the puparium, thereby detaching the anterior end of the puparium and enabling the pharate fly to escape, after which it is withdrawn into the head. Studying and establishing compelling reasons for this unique loss of the ptilinum in the schizophoran families, is of great interest to taxonomists, morphologists and evolutionary biologists alike.

Mc Donnell and Knutson note that all of the species within the *Sepedon* lineage that they examined had well-developed hooks on the labellum (the apical part of the proboscis). These hooks are typically absent in other sciomyzid taxa. They suggest that when present, these hooks assist adult flies to grip and move through the substrate after emerging from the puparium. Mc Donnell and Knutson also postulate that the hooks may have a role in trophallaxis, possibly assisting with the whipping up and handling of orally or rectally produced nuptial gifts, which are presented by *Sepedon* males to females before or during mating (Berg & Valley 1985*a*, *b*). Berg and Valley did not observe trophallaxis in genera of other Sciomyzidae. The possibility that the hooks have a role in other kinds of feeding is also mentioned by Barraclough (1983) and Mc Donnell and Knutson (pers. comm.).

The main objective of the current study was to examine the labellum of commonly encountered South African species of *Sepedon* (subgenera *Mesosepedon* Verbeke and *Parasepedon* Verbeke), to discover whether labellar hooks are present or absent. If hooks were present, additional aims were to discover where they are inserted, and whether the form, orientation and shapes of the hooks differ between species. To date, labellar structures have only been briefly studied in *S. neavei* (Barraclough 1983: 311). A supplementary aim of the study was to review the numbers of hooks in the labellar lobes of the *Sepedon* species studied, and to examine the apparent form of the pseudotracheal rings and intervening interpseudotracheal membrane (see Elzinga & Broce (1986) for further information). It is hoped that the data gathered will encourage and facilitate further studies, and will in addition suggest an array of new characters that may be useful in taxonomic research.

MATERIAL AND METHODS

All material used in the study was sourced from Dr R. Miller (School of Biological & Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg). Relatively commonly encountered species of *Sepedon* with long series were selected, given that very few dry, pinned specimens have suitably everted labella, an essential requirement of the study. Representatives from both commonly encountered subgenera were selected. In addition, a species of *Ethiolimnia* Verbeke—the only other southern African tetanocerine genus—was studied, as was a species of *Ditaeniella* Sack (Sciomyzini). This meant that taxa from both southern African tribes of Sciomyzinae were studied (see also Knutson 1980). Insufficient material of the sole species of the only other subfamily, the Salticellinae, was available for study.

Even with substantial numbers of specimens available, very few had suitably everted labella. The following eight specimens were selected for study (locality data in parentheses). All are from KwaZulu-Natal, South Africa, unless otherwise indicated:

Sepedon neavei, ♂ (Lotus Park, 4 km N Pietermaritzburg, 7.vi.1991)
Sepedon neavei, ♀ (Pietermaritzburg, no other label data)
Sepedon pleuritica, ♂ (Foxhill Spruit, 3 km S Pietermaritzburg, 17.vi.1991)
Sepedon scapularis, ♂ (Lotus Park, 4 km N Pietermaritzburg, 27.iii.1993)
Sepedon scapularis, ♂ (Ukulinga, 8 km S Pietermaritzburg, 28.vi.1991)
Sepedon testacea, ♂ (Foxhill Spruit, 3 km S Pietermaritzburg, 23.vi.1991)
Ditaeniella sp., ♂ (Scottsville, Pietermaritzburg, 13–19.v.1986)
Ethiolimnia geniculata, ♀ (Jeffrey's Bay, Eastern Cape, 2.xi.1978)

To limit damage to the proboscis and labellum, in most instances the entire head was detached using jeweller's forceps, and was attached to a stub (in the appropriate position for viewing) using double-sided tape. In a few cases the entire body of the fly was mounted on the tape. After coating with gold (Polaron E5100 sputter coater), the specimens were examined and photographed using a LEO 1450 scanning electron microscope.

No attempt was made to identify specific sensilla in the interpseudotracheal membrane or elsewhere, as this level of detail was never intended as part of the study. Component structures of the membrane are grossly referred to as papillae.

A single unpublished SEM image from a previous study (Barraclough 1981) was also included in the study. Adobe Photoshop CS2 was used to improve the digital imagery and compile the plates.

RESULTS

Ditaeniella sp.

In this unidentified species there were 15 or 16 pseudotracheae per labellar lobe. The pseudotracheal canal is narrow; the ring tips are depressed and may in fact be difficult to discern. The interpseudotracheal membrane bears no hooks or any other protuberant structures, is virtually smooth, and lacks noticeably differentiated papillae. No attempt was made to study the labellum further.

Ethiolimnia geniculata Loew (Fig. 1)

As with the *Ditaeniella* species, the pseudotracheal canals are narrow and the ring tips depressed, although the tips are more strongly developed. There are no labellar hooks present in the interpseudotracheal membrane or elsewhere. Unlike the *Ditaeniella* species, the membrane does have very weakly differentiated ovoid papillae evident in some areas.

Sepedon neavei Steyskal (Figs 2, 3)

Unfortunately the labella of the suitable specimens were only partially everted, so it was impossible to adequately view all structures, including all of the pseudotracheae in each labellar lobe. It was, however, possible to estimate that there were seven hooks in each labellar lobe. This compares favourably with the eight or nine hooks per lobe previously observed in material of this species (Barraclough 1981). This gives an approximate range of 7 to 9 hooks per labellar lobe.

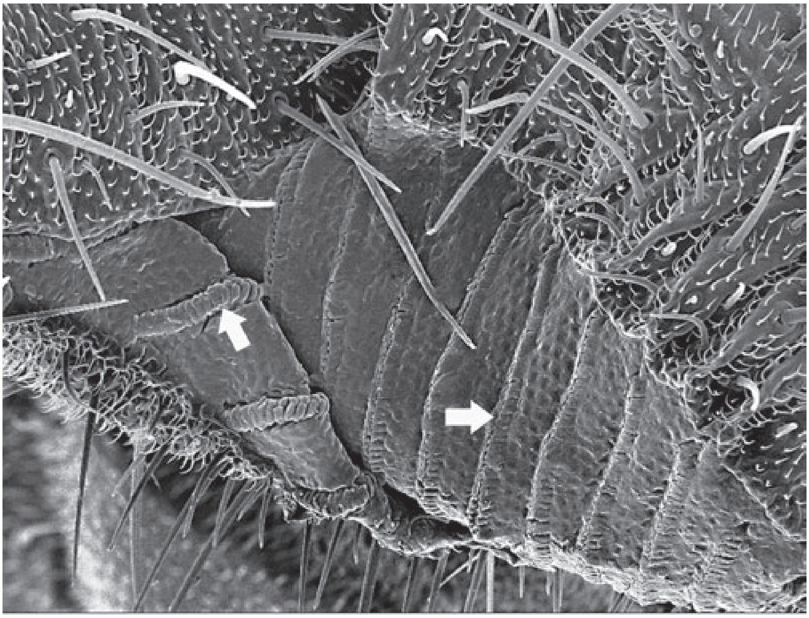


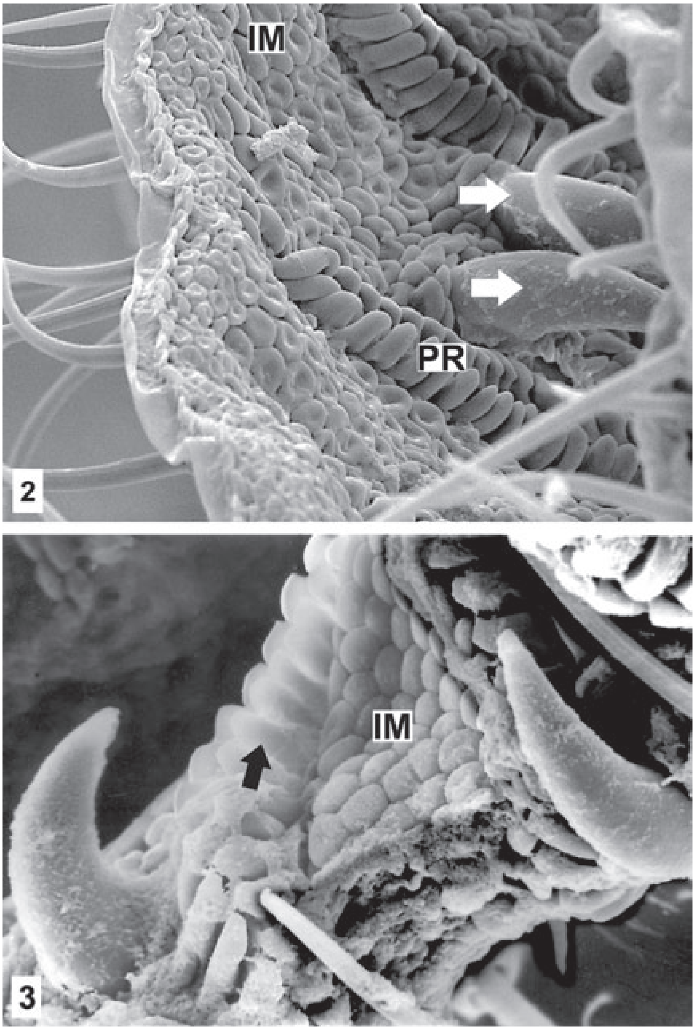
Fig. 1. *Ethiolimnia geniculata*, partially everted labellum, showing inconspicuous rows of pseudotracheal rings (arrowed), with largely undifferentiated interpseudotracheal membrane between the rows. Magnification: 1020×.

In the only previous study referring to labellar structures in southern African sciomyzid flies (Barraclough 1983), the labellar hooks of *S. neavei* were figured and referred to. No additional detail was, however, presented. Note, however, that the hooks were incorrectly identified as prestomal teeth, which are absent from Sciomyzidae.

In the available material, as with all the other *Sepedon* species discussed below, the labellar hooks are large, inwardly directed towards the prestomum, sharply pointed, prominently curved and strongly sclerotised. It is not possible to comment on the presence or absence of smaller hooks. It is evident, though, that there may be two relatively closely approximated hooks *between* a pair of pseudotracheal rows at a particular level. In addition, the hooks are inserted adjacent to or even contiguous with a pseudotracheal row, and typically seem to be inserted in or along upwardly arched contours of interpseudotracheal membrane. This membrane appears not to be structurally differentiated from the remaining membrane, although it may appear so when viewed at certain angles. Labellar hooks never arise from the pseudotracheal rings. The pseudotracheal ring tips are erect and prominently exserted above the surface of the membrane. The circular to ovoid papillae in the interpseudotracheal membrane are strongly differentiated, flattened, and each has a prominent central excavation.

Sepedon pleuritica Loew (Figs 4, 5)

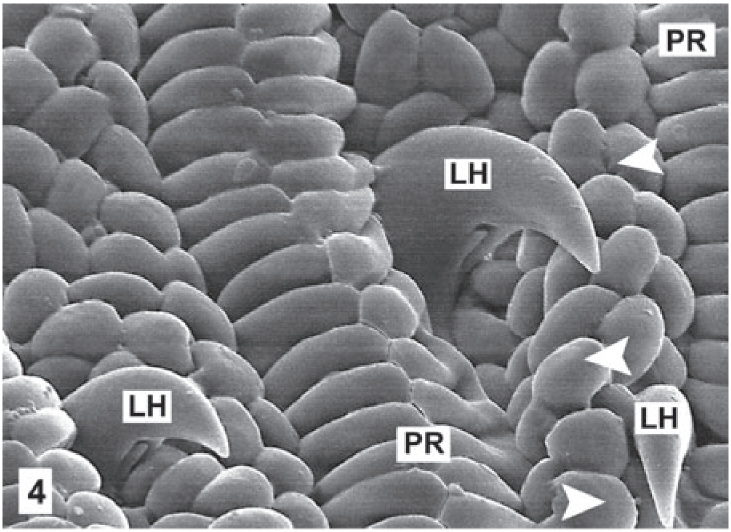
In the available specimen, it was estimated that there were six hooks and 16 rows of pseudotracheae in each labellar lobe. Hooks of different sizes can be present in the membrane of a particular area of the labellum, although typically there is just one hook between each pair of pseudotracheal rows at a particular level. Hooks are always inserted

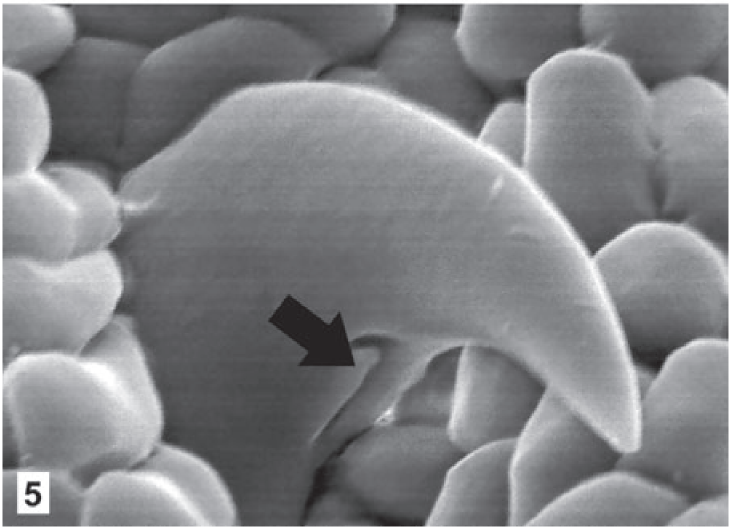


Figs 2, 3. *Sepedon neavei*: (2) labellum, partially everted, showing paired labellar hooks (arrowed), elevated pseudotracheal rings (PR), and interpseudotracheal membrane (IM) with centrally excavated papillae; (3) labellum interior, showing paired labellar hooks in foreground, interpseudotracheal membrane (IM) and pseudotracheal ring tips (arrowed). Magnifications: Fig. 2, 2390×; Fig. 3, magnification details unavailable.

in the membrane adjacent to a pseudotracheal row, but unlike in *S. neavei*, are not always inserted in upwardly flared sections of interpseudotracheal membrane. The pseudotracheal rings are somewhat depressed, and thus are not as prominently exserted above the interpseudotracheal membrane as in *S. neavei*. The ovoid papillae of the interpseudotracheal membrane are strongly differentiated, and somewhat bulbous in appearance, and without any indication of a central excavation.

Of particular interest in *S. pleuritica* is the presence of a small, straight, rod-like structure at the anterior margin of the base of each labellar hook. This structure is present even in very small hooks, where it may exceed half the length of the hook itself.



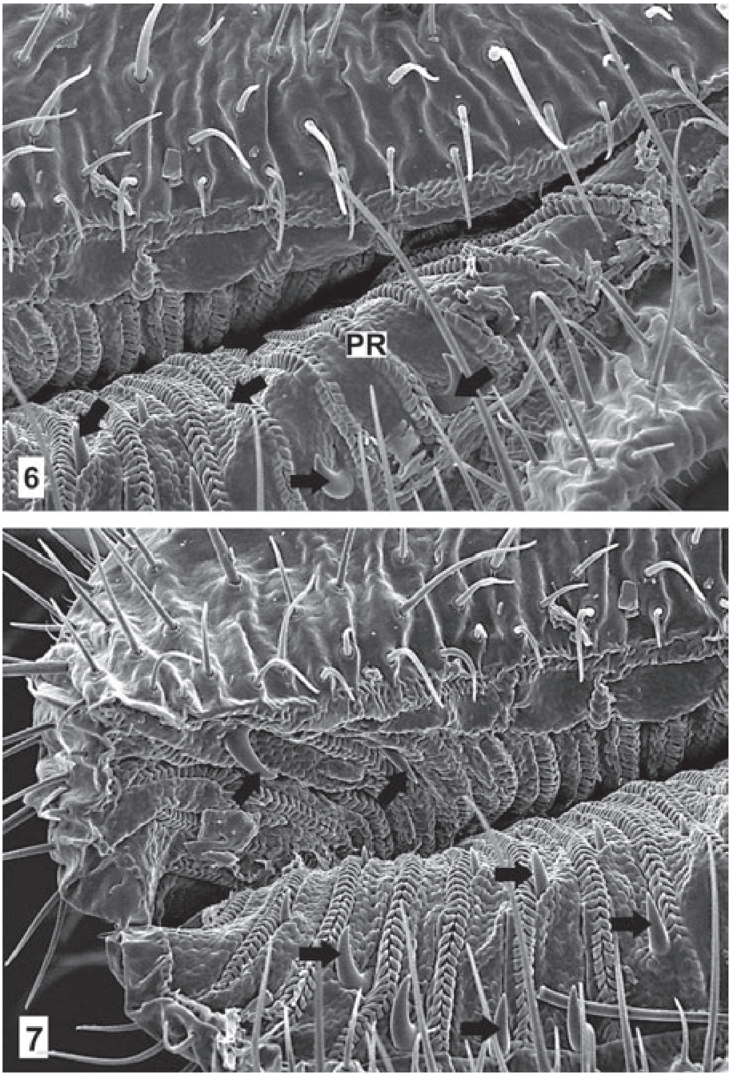


Figs 4, 5. *Sepedon pleuritica*: (4) labellar surface showing distribution of labellar hooks (LH) and depressed pseudotracheal rings (PR), note upwardly furled section of interpseudotracheal membrane (arrow heads); (5) labellar hook, showing basal rod-like structure (arrowed), partially concealed within longitudinal groove. Magnifications: Fig. 4, 2250×; Fig. 5, 5220×.

However, in large hooks it is restricted to about the basal two-fifths, and is positioned entirely within a small, longitudinal excavation.

Sepedon scapularis Adams (Figs 6, 7)

In examined specimens it was estimated that there were 17 hooks and 16 pseudotracheae in each labellar lobe. The development and structure of the hooks, pseudotracheal rings and interpseudotracheal membrane are strongly reminiscent of *S. neavei*, although there seem never to be two hooks between a pair of pseudotracheae at a parti-



Figs 6, 7. *Sepedon scapularis*, partially everted labella, showing pseudotracheal rings (PR) of numerous pseudotracheae, and variously visible labellar hooks (arrowed) in the interpseudotracheal membrane. Magnification: 832×.

cular level, and the papillae of the interpseudotracheal membrane appear to lack a central excavation.

Sepedon testacea Loew (Figs 8, 9)

In the examined specimen, it was estimated that there were 17 hooks and 15 pseudotracheae in each labellar lobe. The hooks are similarly developed and orientated to those found in the other *Sepedon* species, but differ from all of them in that they are typically differently positioned, i.e. inserted parallel to the pseudotracheal rows, sometimes midway between a pair of rows. Also unlike all three other species, the small irregularly-shaped papillae of the pseudotracheal membrane are more flattened, and each is separated from the other by a groove-like depression in the surface. The papillae typically do not have a centrally excavated area. Another point of difference from the other species is that there are significant amounts of interpseudotracheal membrane where no differentiated papillae are evident.

DISCUSSION

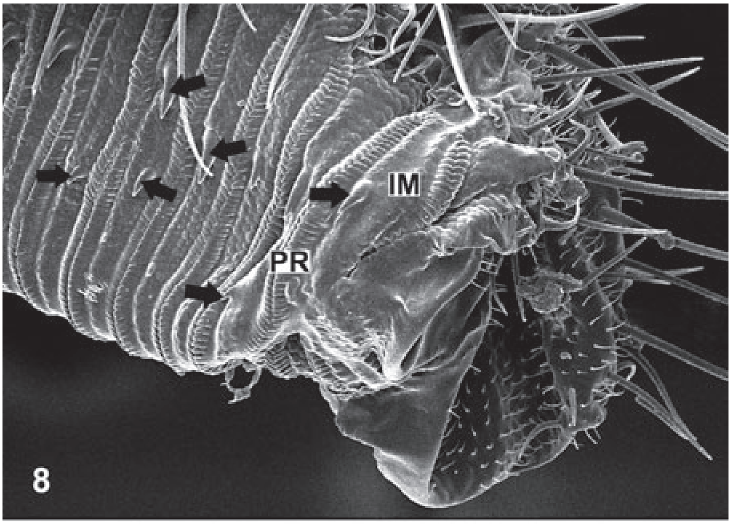
My study confirms the presence of labellar hooks in the interpseudotracheal membrane of all four species of *Sepedon* examined, and their absence in *Ditaeniella* and *Ethiolimnia*. As both *Ditaeniella* and *Ethiolimnia* have a ptilinal suture, and the four *Sepedon* species lack it, my study confirms that the presence of labellar hooks is an apomorphy, correlated in some way with the loss of the ptilinum (Mc Donnell & Knutson pers. comm.). It was not the purpose of this study to comment on any additional morphological or behavioural adaptations in *Sepedon* species.

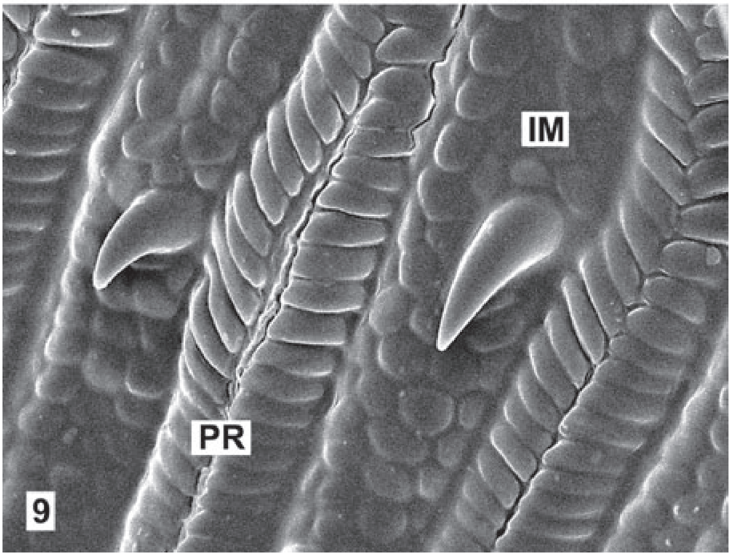
All the labellar hooks were similarly developed, orientated, sclerotised and shaped, although a variety of sizes typically occur in each species. However, the number of hooks per lobe varies dramatically between some species. Both *S. scapularis* and *S. testacea* had about 17 labellar hooks in each labellar lobe, while there were far fewer hooks per lobe in *S. neavei* (7 to 9), and *S. pleuritica* (6). The implications of these differences are not known, but the numbers of labellar hooks per lobe appear to be species-specific, and thus could be of taxonomic significance.

Of interest is that labellar hooks may be inserted close to or even contiguous with pseudotracheal rows in most species (*S. neavei*, *S. pleuritica*, *S. scapularis*), but are usually inserted away from the rings in *S. testacea*. An important consideration is that labellar hooks *never* arise from pseudotracheal ring tips. Also of note is that the former three species have upwardly arched contours of interpseudotracheal membrane, unlike *S. testacea* where the membrane is almost uniformly flat and lacks differentiation into papillae in some areas.

Sepedon pleuritica (Figs 4, 5) differs from the other three species in having a small rod-like structure positioned vertically along the anterobasal margin of each labellar hook. This structure is evident in hooks of all sizes, and is proportionally larger in smaller hooks. Although its function is not known, it may have a supportive function of some kind. The morphology of this structure, and this area of the labellar hook, warrants further study, as the presence or absence of the structure may be of some taxonomic significance (*S. pleuritica* belongs to the subgenus *Mesosepedon*, the other species to *Parasepedon*). It should be noted, however, that the anterobasal area of the labellar hook is unusually difficult to view in many preparations, rendering study difficult.

Although not intensively studied, the form and development of the pseudotracheal rings and associated interpseudotracheal membrane may offer characters of value in future taxonomic studies. No noticeable microteeth were observed on the pseudotracheal ring tips, although further study is required. *Sepedon neavei* and *S. pleuritica* have fewer pseudotracheae (6 or 7), whereas they are much more profuse (17) in *S. scapularis* and *S. testacea*. Within *Sepedon* the pseudotracheal ring tips are variously exserted above the membrane, and the papillae of the interpseudotracheal membrane are differently shaped, structured and differentiated. All these differences appear to be species-specific, and it would be of great interest to focus on them in future morphological





Figs 8, 9. *Sepedon testacea*: (8) labellum, everted, showing labellar hooks (arrowed), depressed pseudotracheal rings (PR) and interpseudotracheal membrane (IM); (9) labellar surface, showing depressed pseudotracheal rings (PR) and interpseudotracheal membrane (IM). Note the insertion of the hooks in membrane away from the pseudotracheal rings, as well as the conspicuous grooving between the papillae in the interpseudotracheal membrane. Magnifications: Fig. 8, 299×; Fig. 9, 1570×.

studies. In the genera *Ethiolimnia* and *Ditaeniella* the pseudotracheal rings and membrane are unremarkable, with a notable depletion of discernible papillae, and the pseudotracheal rings are not elevated much above the surface of the membrane.

It is imperative that further studies on the labellum of sciomyzid flies are undertaken in the future, to support and build on the data set presented here. This should include examining longer series of specimens, specimens of both sexes, and additional representative species.

Such species should include, for example, the rarely encountered genus *Salticella* Robineau-Desvoidy, and within *Sepedon* the subgenus *Sepedomyia* Verbeke. In addition, techniques need to be developed—preferably when collecting fresh material—to ensure that the labellum is fully everted, and thus suitable for study.

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